Bound for Specific Sounds: Vocal Predisposition in Animal Communication

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Bound for Specific Sounds: Vocal Predisposition in Animal Communication

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Mechanical constraints imposed by anatomical adaptations are a ubiquitous feature of animal sound production. They can give rise to 'vocal predispositions' (i.e., acoustic structures strictly determined by vocal anatomy). Such predispositions are crucial to the investigation of the cognitive and evolutionary processes underlying acoustic communication in vertebrates, including human speech.

Introduction

Uncovering the origins and evolutionary forces shaping acoustic signals has been a central focus of animal communication research. In line with the Darwinian concept of adaptation, and facilitated by the generalization of phylogenetic analysis methods, recent advances have identified how sexual and environmental pressures act on signals' design. In response to such pressures, modifications of vocal apparatuses (i.e., anatomic adaptations) strongly contribute to the acoustic diversity found in animal signals [1]. In parallel, assessment of the cognitive requirements associated with various aspects of vocal communication (including sound production, perception, and processing) has proved a critical approach to comparative work investigating the evolution of communication systems, including that of human speech [2–4]. However, to what extent can anatomic adaptations predetermine vocal outputs, thereby potentially either limiting or outweighing the role of cognitive control over sound production? We address this question in light of the most recent breakthroughs in the fields of bioacoustics and comparative linguistics [additional references are listed online (see the supplementary information online)]. We define 'vocal predispositions' as a range of acoustic features predetermined by species-specific vocal anatomy. We emphasize why identifying vocal predispositions is essential to infer evolutionary histories and the cognitive processes underlying the structure and use of acoustic signals.

Anatomical Adaptations Generate Vocal Predispositions

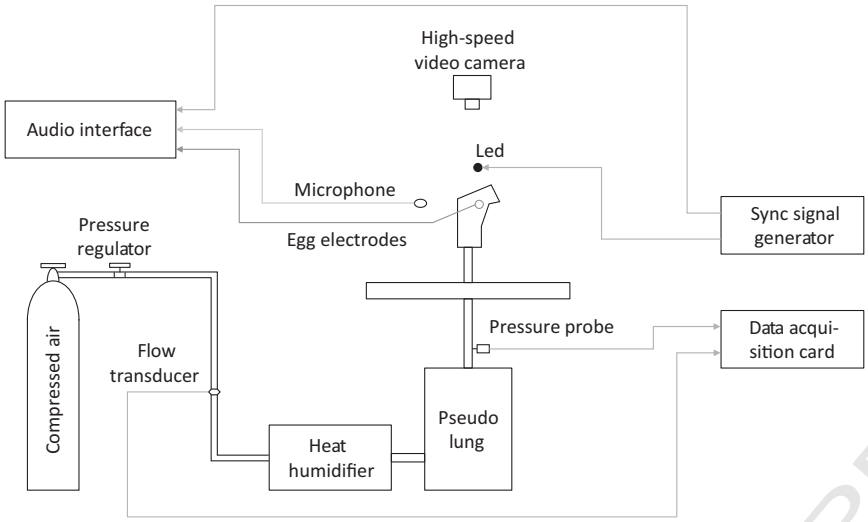
Acoustic communication has evolved as a behavioral keystone in most of the animal taxa. Across vertebrates, sound-generating organs come in diverse forms and are often characteristic of the clade considered: Typically, birds produce calls with a syrinx, while mammals and amphibians do so using their larynx, and fish their swim bladder [5]. However, deviations from typical structures occur in each of these clades to varying degrees as a result of various selective forces. Modifications of the vocal apparatus can, for instance, originate from sexual selection, as seen in the context of dishonest signalling: Here, changes in vocal anatomy result from an attempt to exaggerate the conveyed impression of body size [1]. Environmental factors can also selectively operate on acoustic features by triggering adaptive changes in a species' vocal anatomy. For instance, there is suggestive evidence that some terrestrial vertebrates have evolved air sacs as an impedance-matching system for sounds to better radiate into their surrounding medium, a function similar to that of phonic lips and melons in several aquatic mammals [5].

Such selection pressures have led acoustic signals to inherently contain a range of features that may not be physically reproducible by other species (e.g., the low fundamental frequencies produced by howler monkeys or the low formant frequency spacing achieved by red deer stags [1]). In other words, vocal predispositions emerge from the biomechanical properties of the sound-generating apparatus available to each species. While this seems obvious, it represents a critical – but often neglected – basis for frameworks investigating the various levels of neural control shaping acoustic signals [6].

Sound Production with or Without a Brain

Understanding how vocal anatomy physically bounds sound production can strongly affect our interpretation of the cognitive underpinnings of acoustic communication systems. The biomechanical properties of sound production organs can generate complex acoustic patterns despite simple input conditions devoid of neural control. For instance, naturally occurring vocal sequences in squirrel monkeys can result from nonlinearities (register breaks and rapid transitions between acoustic patterns or call types) that are intrinsic to laryngeal biomechanics in this species [7]. In this example, vocal sequence generation thus results from vocal predispositions and does not require advanced neural control. Experimental designs aimed at phonating excised vocal apparatuses *ex vivo* (hereafter 'EVAE' for 'excised vocal apparatus experimentation') provide an ideal tool to investigate this topic. Free from any neural control, this type of approach provides a biomechanical baseline on which to build inferences about the cognitive processes associated with vocal motor control (Figure 1).

As part of the research exploring these cognitive capacities supporting communication, vocal production learning (VPL; referred to as the ability to imitate or modify existing vocalizations to produce noninnate vocal signals) has received particular attention. VPL requires advanced motor control over vocal organs [8] in order to produce the spectral and/or temporal modulations typical of vocally learned signals (e.g., [9]). In vertebrates, VPL is found in many birds



Q1 Figure 1. *Ex Vivo* Study of Sound Production. A schematic illustration of an experimental excised larynx setup (adapted from [12]). Excised larynx experimentation (ELE; similar to excised syrinx experimentation in birds) consists of phonating a larynx *ex vivo* by driving pressurized air through it. ELE allows investigating sound production mechanisms while parceling out neural control. Combined with dissections, this approach reveals the biophysical behaviour of species-specific larynges and thus provides direct insight into vocal predispositions. As an example, ELE is a highly promising tool to disentangle the origin of nonlinear dynamics (NLD) occurring in animal sound production. NLD depend on a combination of input parameters (such as subglottal pressure and vocal fold tension), but not all larynges behave similarly with regard to NLD production. Research in this area can help improve understanding of whether NLD are evolutionary by-products or functional adaptations, which is essential to quantify vocal repertoires and determine the degree of volitional control on acoustic structure and use of vocalizations. Extending excised experimentation to the upper vocal tract will strongly complement computational modelling of dynamic filter-related vocal features and is a promising frontier that bioacousticians should tackle in the future. Abbreviations: LED, light emitting diode.

and few mammalian clades (including humans), and its assessment commonly relies on comparative approaches. Anatomic constraints are a major component determining the outcome and interpretations of comparative VPL research, as illustrated by theoretically comparing humans and lyrebirds, two species with advanced VPL abilities. Humans are unlikely to rival lyrebirds that mimic sounds of chainsaws, camera shutters, or other bird species' songs (https://www.youtube.com/watch?v=mSB71jNq-yQ); yet, one should not conclude that humans are not vocal learners, but rather that neural pathways [9] and vocal organs significantly differ in these clades. The same consideration of vocal motor control being contingent on vocal predispositions should always apply to avoid downplaying or inflating cognitive performances associated with VPL when comparing different taxa. In line with this, the use of stimuli matching the range of physical capabilities of species-specific vocal apparatus should be paramount in VPL research (Figure 2). This will be possible only through careful evaluation of vocal predispositions and considering VPL as a continuum [4].

A flagship study field illustrating advances made by considering vocal predispositions is that of language evolution, as highlighted by recent work showing that human speech can be shaped by biomechanical adjustments to dietary practices, such as bite configuration [10]. Comparative work also showed that the anatomic constraints imposed on monkeys' vocal tract were not responsible for the lack of speech emergence in our close relatives. Instead, the dual consideration of vocal anatomy and neural control provides compelling evidence that the missing element is a speech-ready brain to control their vocal tract [2]. Similarly, a study controlled for sound production biomechanics to demonstrate that marmosets' brain circuitry contributes to vocal development in this species, as with the mechanism in place for vocal learning emergence in humans [3]. Finally, contrasting the mechanisms responsible for speech production with those involved in the production of non-verbal vocal communication has been suggested as a promising research avenue, as it will help improve understanding of volitional vocal control in humans [11]. These integrative approaches illustrate how much benefit can result from considering anatomic constraints in the study of our own language, including when developing new testable frameworks [6].

Vocal Predispositions Towards a Predictive Framework

Although the general shape of sound production structures has remained relatively conserved within clades, vocal adaptations in response to natural and sexual selections are widespread. Furthering our understanding of vocal predispositions (i.e., the acoustic signals' properties that derive from interspecific anatomical variation) has potential to open new pathways for animal vocal communication research. In particular, we argue that future research should focus on identifying the range of – and, even more relevant, the differences between – expected and observed vocalizations, given species-specific vocal anatomies. This approach can advance our understanding of unique vocal features by helping to identify the anatomic correlates of species-specific vocal traits. Building on predictions (via vocal anatomy modelling, EVAE, and knowledge from related species) while conducting cross-species comparisons, deviations from the norm (observed = expected) can

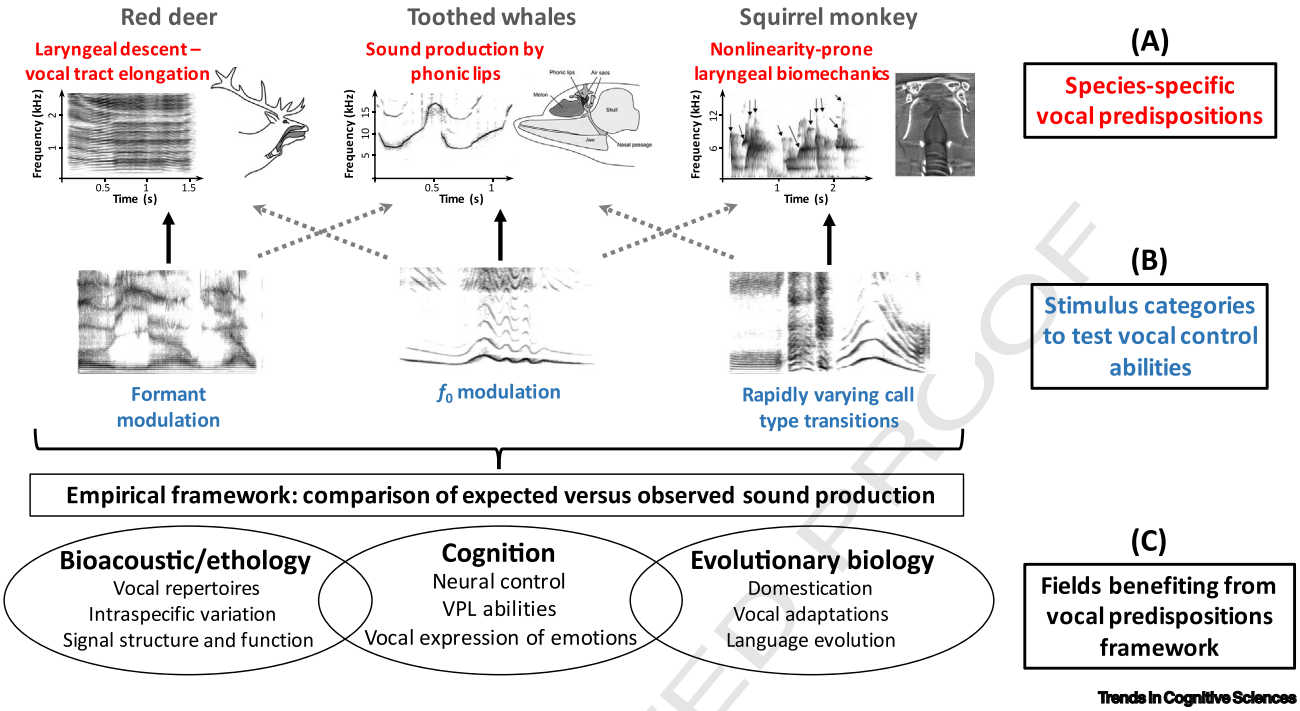


Figure 2. Importance of Anatomic Constraints in Vocal Communication Research. (A) Anatomic adaptations and sound spectrograms highlighting vocal predispositions (in red) in three exemplar species' communication systems. For each species considered, acoustic signal structure is predetermined by vocal anatomy; we thus find formant lowering in red deer calls as they elongate their vocal tract, highly tonal signature whistle produced through phonic lips in toothed whales, and abrupt frequency jumps in a call sequence of squirrel monkeys, inherent to their laryngeal propensity for such jumps. Red deer illustration: courtesy of Tecumseh Fitch; toothed whale illustration: adapted from [5] and courtesy of Livio Favaro (audio available as supplementary material; see supplementary information online); squirrel monkey illustration: adapted with permission from [7], with arrows indicating successive elements in a vocal bout. (B) Hypothetical study testing vocal production learning (VPL) abilities in different species: This requires choosing appropriate stimuli (in blue) (i.e., stimuli tuned to the tested species' vocal predispositions). Naturally occurring vocalizations should help select or design biologically relevant experimental stimuli [formant modulation in red deer; fundamental frequency (f_0) modulation in toothed whales; and nonlinear phenomena (changes in vocal fold vibratory regimes) in squirrel monkeys]. Solid arrows indicate the preferred stimulus to choose, given a model species' vocal predispositions. Dashed arrows indicate possible – but less appropriate, as potentially less in line with the model species' vocal predispositions – alternative stimuli. (C) Research areas that will benefit from adequate consideration of the vocal predispositions found across species.

potentially indicate restrained behavioral use of vocalizations (observed < expected) or greater than average vocal motor control (observed > expected). Reflections on (and empirical testing of) the mechanisms responsible for such expected/observed differences can therefore provide critical insights into the volitional versus uncontrolled origin of acoustic signals and the relative influence of the selective pressures driving the evolution of acoustic communication systems.

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Supplementary Information

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